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Sensitivity of upland arthropod diversity to livestock grazing, vegetation structure and landform

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Abstract
Livestock production extends to most non-forested, marginal, upland habitats of Britain. Of these, indigenous grasslands are stocked predominantly by sheep, stocking densities having increased in Scotland by 25% between 1975 and 1990. Conversely, the national herd of cattle in Scotland declined by 22% over the same period. The effects of grazing management on arthropod distribution and abundance is reviewed, with particular emphasis on the results of grazing experiments that have investigated the effects on arthropods of varied livestock species and stocking rates. Arthropods contribute the most species of any taxa in the uplands and are critical in upland food chains. The direction and magnitude of the response of different arthropod taxa to grazing management reflects their trophic level, life history, size and mobility, e.g., 30 % of ground and rove beetle species are more sensitive to landform than grazing management. For the arthropod taxa that are sensitive to grazing management, the effects are generally indirect, via changes in the heterogeneity of botanical composition and vegetation structure. A mosaic of contrasting botanical composition and structural heterogeneity is essential to conserve and enhance arthropod and broader wildlife diversity in the uplands. However, the landscape-scale study of mammalian herbivore-vegetation-arthropod interactions is required both to quantify the relative importance of land use (grazing management) and landform (landscape physiognomy) across the uplands and to determine the optimal grain-size of the habitat mosaic to sustain biodiversity.

Key words: Livestock production, sheep grazing, cattle grazing, indigenous grasslands, upland, biodiversity, insect diversity and spider diversity.

Introduction
Substantial increases in *Ovis aries* (sheep) numbers in upland areas of Britain from the 1970s-1990s (2 million or 25%) have placed significant pressure on indigenous grasslands in the uplands [1]. There has been a 600 000 or 22% decline in *Bos taurus* (cattle) across all farmland over the same period, indicating a trend from mixed grazers to sheep only. Grazing beyond sustainable intensities by sheep, *Cervus elaphus* (red deer) and *Oryctolagus cuniculus* (rabbits) has also increased grassland at the expense of heathland vegetation dominated by *Calluna vulgaris* (heather) [2,3,4,5,6]. Hence, many uplands are currently grass- rather than heather-dominated [7] although the arthropod fauna of indigenous grasslands can also be diverse compared with alternative biotopes [8,9]. Indigenous upland grasslands also have a greater importance today because the species shared with lowland grasslands have been diminished by intensification of management in the lowlands [10] Upland grasslands vary in their botanical composition although there is a predominance of acid grasslands composed of *Agrostis* and *Festuca* species with dominance by *Nardus stricta* in drier areas and *Molinia caerulea*, *Eriophorum* or *Scirpus* species in wetter areas [11]. Research on grassland arthropods has largely focused on lowland, calcareous grasslands because of the higher botanical diversity compared with upland, acid grasslands [12] and the distinct arthropod species rather than diversity *per se* [12,9]. However, there are substantial areas of karst and small calcareous flushes in the uplands and these have an important arthropod fauna associated with them [13,14]. The extensification of pasture management is considered a means of integrating biodiversity conservation with agricultural production objectives for the broader upland grassland types and for achieving a restoration of heather moorlands [15].

Arthropod diversity - so what?
Typically, arthropods contribute well over half the metazoan species in any habitat or ecosystem [16]. Beyond the numbers argument, arthropods occupy several trophic levels and fulfil vital functions within ecosystems that can be summarized under particular socio-ecological headings [17,18]. Certain species have utility value as natural enemies of potential pest herbivores in grasslands and heathlands. For example, the ground beetles, *Carabus* spp. and *Cychrus caraboides* (Coleoptera: Carabidae) are mollusc predators, the smaller but closely related *Notiophilus aquaticus* specializes on springtails (Collembola) that includes the pest, *Sminthurus viridis* [19]. Many herbivorous insects are not pests but they do consume plant material and return nutrients to the soil, hence reducing litter accumulation. They also provide food for higher trophic levels (predatory insects, insectivorous mammals and birds). Some Diptera (frit flies and craneflies), Coleoptera (leaf beetles, weevils and wireworms) and springtails (*Sminthurus viridis*) can be occasional pests in intensively managed grasslands although this is unknown in indigenous grasslands.

There has been more general scientific interest (ecologistic-scientific value) in what arthropod species do in ecosystems [18], particularly inspired by evidence of declines in abundance of many species and questions of what the consequences might be for ecosystem function. The productivity and maintenance of fertility in soils is one critical area, dung beetles prevent pasture fouling and enhance the cycling of nutrients, whilst bumblebees ensure the successful pollination of many flowering species. The ecologistic-scientific value extends to the role for arthropods as contributors to the diet of other species of conservation value. Leatherjackets, larvae of craneflies (Diptera: Tipulidae), represent the largest invertebrate biomass in the uplands and significantly contribute to the diet of the rare upland Dotterel, *Eudromias morinellus* (Charadriidae) [20] and the economically important Red grouse, *Lagopus lagopus* [21]. Large beetles, such as *Carabus* spp. (Col.: Carabidae) and Dor beetles (Col.: Scarabaeidae) make a contribution to the diet of birds of prey such as the Merlin, *Falco columbarius* (Falconidae) [22]. Finally, the naturalistic, aesthetic value of the more charismatic species of insects is self-evident but highly selective. The Scotch Argus butterfly, *Erebia aethiops* (Lepidoptera: Satyridae), Emperor moth, *Saturnia pavonia* (Lep.: Saturnidae), Burnet moths, *Zygaena* spp. (Lep.: Zygaenidae), and dragonflies and darters, *Aeshna juncea* and *Sympetrum danae* (Odonata) are typical examples (UK Biodiversity Action Plan [16]).

The importance of Spatial Scale

It is important to take account of the ways in which spatial scale impinges on large herbivore-arthropod interactions. Certainly, large herbivores interact with vegetation at three identifiable scales: the feeding station, vegetation patch and landscape [23]. The relative effects of large herbivores on arthropods varies according to the scale of observation because:

- large herbivores do not uniformly forage everywhere [4,24].
- plant communities, and their availability and response to grazing [25, 26], are not constant due to variability in landform, hydrology and climate[11] .

Aspect, gullying and wet pockets alter the dominance of vegetation at constant altitude around hills and, in addition, altitudinal gradients in upland terrain are related to shifts in vegetation communities from dry grasslands, to heather and weathered peatlands or montane vegetation on skeletal soil on the high plateaux [11], all of which create different upland arthropod assemblages [27,28]. This paper reviews the findings from several experiments across Scotland that investigated arthropod responses to varied grazing management [29,30,31,32]. The results of the grazing experiments are placed in the context of other grazing studies of upland and indigenous habitats [33,34, 35,36, 37,38].

Grazing Management on Upland Plant Communities

The research refers to several experiments that were conducted between 1993 and 1998 which had in common grazing by sheep, in one case cattle also, and all grazed to achieve a selection of target average sward heights, representing a spectrum of grazing intensities designed to match the productivity of each site. The site habitats defined according to Ratcliffe[8] and given National Vegetation Classification (NVC) classes of Rodwell [11] included:

- *Agrostis-Festuca* equivalent to NVC U4e grazed by sheep to maintain 3, 4.5 and 6 cm sward heights, plus an ungrazed control, Cleish Hills, Fife.
- *Festuca-Agrostis* equivalent to NVC U4a grazed by sheep to maintain 3, 4.5 and 6 cm sward heights, plus an ungrazed control, Tyndrum, Highlands.
- *Nardus stricta* equivalent to NVC U5a grazed by sheep and cattle (June to August) to maintain 4.5 and 6.5 cm sward heights, plus an ungrazed control, Cheviot Hills, Scottish Borders.

Sampling arthropods and vegetation

Data collection of arthropods included the use of suction sampling for leafhoppers and web-spinning spiders on vegetation [30], and pitfall trapping to sample surface-active beetles (Coleoptera) [29,31], spiders (Araneae) and harvestmen (Opiliones) [31]. Sward height profiles were measured around all arthropod-sampling points to provide data on spatial heterogeneity (patchiness) of the upland habitats [30].

Distinguishing Direct/ Indirect Effects of Grazing Herbivores From Abiotic Influences on Arthropods

The interactions between grazing herbivores and vegetation and the magnitude of their influence on arthropods depends on geographical context. Complex landform is symptomatic of upland areas. Altitude, aspect and slope vary markedly to produce different patterns of insolation and soil wetness. For example, the topographic gradients of chalk grasslands revealed as much variance within-site as along a latitudinal gradient in England [39] . To place the effects of grazing herbivores on arthropods into context it is necessary to consider local biotic mechanisms and to interpret them with regard to broader environmental conditions.

Table 1. Turnover in dominant leafhopper and plant bug species of upland plant communities(● indicates presence).

Plant community (NVC)	U4a *Festuca-Agrostis*	U4e *Agrostis-Festuca*	U5a *Nardus stricta*
Leafhoppers - Homoptera			
Javasella discolor	●		●
Dikraneura variata		●	
Diplocolenus abdominalis	●		
Aphrodes bifasciatus		●	●
Plant bugs – Heteroptera			
Pachytomella parallela	●	●	●
Halticus apterus	●		●

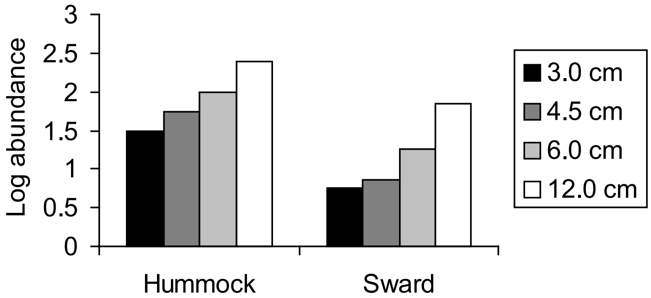

Figure 1. Abundance of planthoppers (Homoptera: Auchenorrhyncha) in contrasting structural components of a patchy *Agrostis-Festuca* grassland (National Vegetation Classification U4e) grazed to different sward heights (after Dennis *et al*[30]).

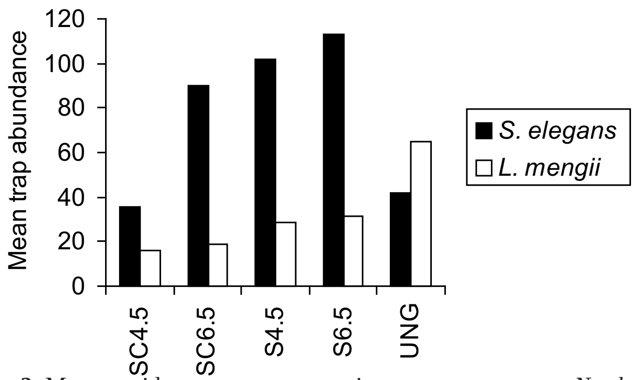

Figure 2. Money spider responses to grazing management on a *Nardus stricta* grassland (S: sheep, C: cattle, UNG: ungrazed and numbers refer to target average inter-tussock sward height of treatment, cm).

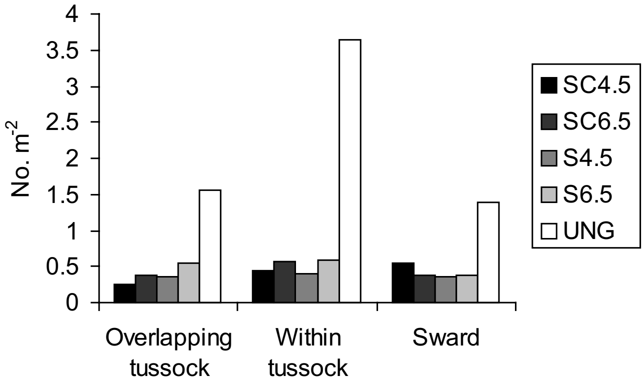

Figure 3. Web numbers in microhabitats under different grazing regimes applied to a *Nardus stricta* grassland. Legend defined in Fig. 2 caption (afterDennis et al.[30]).

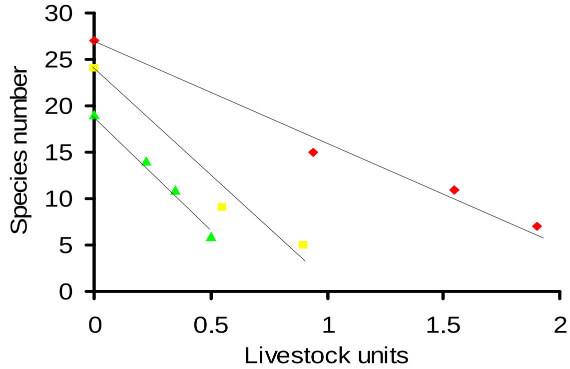

Figure 4. Leafhopper and plant bug species responses to sheep grazing intensity on different plant communities.Key: triangles, *Festuca-Agrostis*, U4a; squares, *Agrostis- Festuca*, U4e and diamonds, *Nardus stricta*, U5a communities.

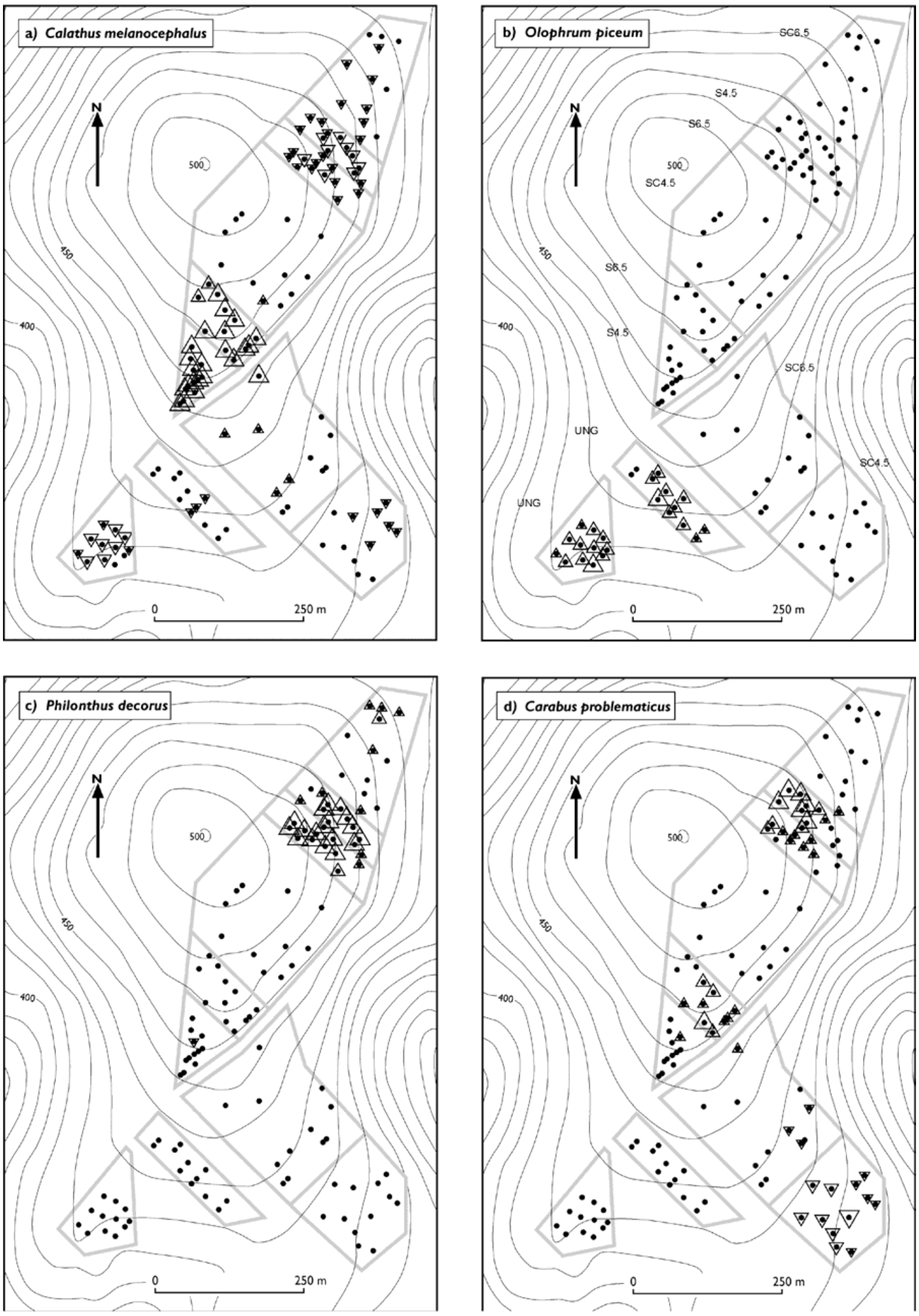

Figure 5. Size and location of clusters of high and low numbers of ground and rove beetles on *Nardus stricta* grassland under varied grazing management (after Dennis *et al.*,[32]). Grazing treatments indicated on b, where S: sheep; C: cattle; UNG: ungrazed for 2-3 years; and, 4.5 and 6.5 represents average between-tussock sward height (cm). Upward pointed triangles represent aggregations of high value and upturned triangles aggregations of low numbers (where $P_{G(z)} \propto$ size; Getis and Ord[63]).

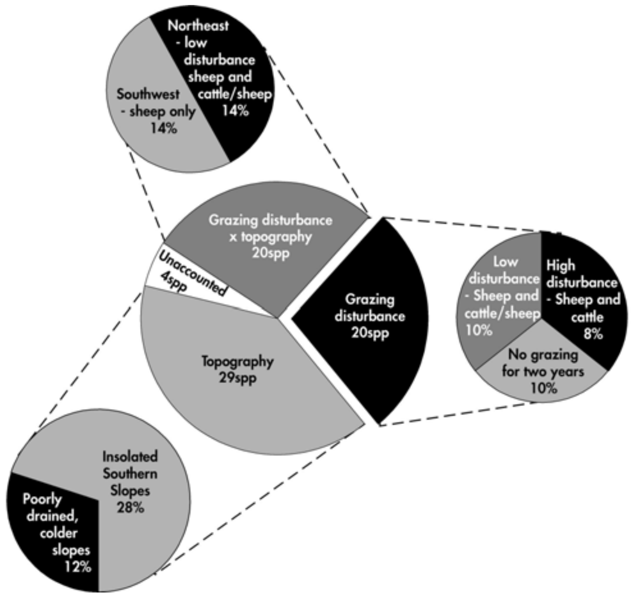

Figure 6. The response of Coleoptera (Carabidae and Staphylinidae) species to grazing disturbance, topography and an interaction between these factors on upland *Nardus stricta* grassland. The 73 species of the assemblage were associated with each factor according to their inter-correlation in a community ordination and the scale and direction of response of indicator species using geostatistical analysis (Dennis *et al*[30]). The satellite circles illustrate the direction of response of the species related to each factor.

Plate 1. Structural differences in *Nardus stricta* grassland after three years of contrasting grazing management, i. sheep grazed May to October to maintain a 6.5 cm inter-tussock sward, ii. sheep, May to October, with cattle, June to August, grazed to maintain a 4.5 cm inter-tussock sward.

Localised selection of preferred plant species

Small, insect herbivores, namely leafhoppers (Homoptera: Auchenorrhyncha) and other plant bugs (Heteroptera) select for particular species or groups of plants[40, 41]. Particular species will therefore associate with upland communities where these host plants are abundant (Table 1) and direct competition between large herbivores and these insects will occur when grazing selects those host plants and reduces their abundance within a particular upland community [42].

Structural heterogeneity of vegetation and insect diversity

Grazing herbivores have an indirect effect on many arthropods by modifying the structural characteristics of upland habitats [30]. The structural appearance of vegetation can be dramatically altered by grazing regime, more so than plant species composition (Plate 1)[43,44,45]. The development of distinct tussock or hummock and sward components has consequences for the distribution of small arthropods, both leafhoppers and spiders [30]. These structural components of grasslands contributed to arthropod species diversity. More individuals and species of leafhoppers were sampled in the taller, more complex components of grasslands, either tussock or hummocks (Fig. 1). Further, the impact of increased grazing intensity on these insects was, somewhat, buffered by these structures (Fig. 1).

If we consider predators requiring architectural diversity for the anchorage of webs, e.g., the money spider, *Silometopus elegans*, its general abundance increases where there is a lower grazing intensity but declines where grazing is absent for over two years (Fig. 2). By contrast, the common money spider, *Lepthyphantes mengii*, demonstrates a similar trend except that the highest catches were in the ungrazed *Nardus stricta* (Fig. 2). The difference is caused by the different locations of web building by these spiders. *Lepthyphantes mengii* constructs webs high in the leaves of tussocks or hummocks and this microhabitat is increased where grazing ceases for longer periods (Fig. 3). Taller swards were the most influential factor, typically being patchier, i.e., having greater variability in sward height [30].

Effects of landform as opposed to solely grazing management

The uplands represent complex terrain and it is important to disentangle direct/indirect effects of grazing management from variability imposed by landform. Slope and aspect create different patterns of insolation and soil wetness [39]. Snow cover can be prolonged on north-facing slopes at higher altitude.

There was an interaction between grazing intensity and environmental conditions for leafhopper and plant bug species indicated by the consistent declining numbers with increased stocking density (Fig. 4). There were fewer potential species on the less productive vegetation at high altitude, on wet, cold slopes, e.g., *Festuca-Agrostis*. In addition, there was greater sensitivity of the plant bug species to grazing intensity on the sites of lower productivity (Fig. 4). Ground and rove beetles (Coleoptera: Carabidae, Staphylinidae), predatory species that roam around on the ground over tens of metres, were sampled at 120 points where pitfall traps were placed within the grazing experiment on *Nardus stricta* (U5a community). A geostatistical procedure was used to determine the size and location of clusters of high and low numbers of beetle species representative of the main trends of all the species[29]. Four distinct patterns were identified that accounted for the main trends expressed by all species and the ecological interpretation identified the relative influences of landform and grazing management (Fig. 5). A large south-facing cluster that extended over several contrasting grazing treatments characterized *Calathus melanocephalus* (Col.: Carabidae; Fig. 5a), and indeed this species is typical of productive lowland pastures. There was also a large cluster across contrasting treatments for *Philonthus decorus* (Col.: Stapylinidae; Fig. 5c) and this showed the selection of more northern conditions typified by soil of greater wetness and organic matter content. The remaining two species both suggested responses to the patterns of grazing. *Olophrum piceum* (Col.: Staphylinidae) had clusters only within the ungrazed plots (Fig. 5b), and this probably relates to the increased litter and associated fungi that would develop in the absence of grazing. The clusters of high numbers of the large species, *Carabus problematicus* (Col.: Carabidae) associated with the sheep rather than sheep and cattle grazed plots (Fig. 5d), and this suggests that there are effects of cattle, possibly through soil compaction or direct treading disturbance, that are detrimental to this species. *Carabus* spp. depend on soil crevices as daytime refugia to avoid desiccation and predation, and the availability of these features may be reduced under cattle grazing. Herbivores affect soil by compacting it where they tread and altering its nutrient status where they produce dung and urine. This directly affects soil insects and arachnids and indirectly affects foliar insects and arachnids by changing plant species composition through changes in soil status, as opposed to forage selection during grazing. Trampling is seen as generally harmful to the arthropod fauna [64], although dung deposition provides a niche for additional species [28].

The patterns of indicative beetle species from the geostatistical analysis[32], and management and environmental correlations of their distributions using direct gradient analysis, allowed a classification of the broader assemblage of 73 species of ground and rove beetles (Fig. 6). A total of 28% of the beetle assemblage was sensitive to the effects of grazing (indicated by partitioned slice), 40% to landform, 28% sensitive to an interaction between grazing and landform and with the remaining 4% unallocated (Fig. 6). The smaller satellite circles indicate the direction of the response of these beetle species to each factor (Fig. 6). Sanderson et al.[46] provide further evidence of the importance that abiotic factors have in affecting the spatial patterns of arthropod populations in upland landscapes at larger spatial scales. Soil moisture or site wetness is recognized as a major determining factor in the distribution of many ground beetle species[10].

Conclusions

There were significant effects of grazing on the species of various arthropod taxa, consistent with other investigations [47,48]. Sensitivity to grazing management is related to taxon and trophic level. The most marked direct effects were on small, herbivorous leafhoppers. Vegetation structure was important for small, herbivorous species and these indirect effects from grazing also influenced the distribution of webs and species composition of web-building spiders. The effects of grazing on the larger, ground-active beetles, namely ground and rove beetles, and wolf spiders was not consistent. About a third of beetle species significantly responded to differences in grazing management. However, landform was a considerable influence on these wider ranging, generalist predators. Overall, it is possible to distinguish between those species primarily sensitive to land use (represented by grazing) and to landform (particularly as it relates to climate change). Clearly, botanical composition and structural heterogeneity are important considerations in the objective to conserve or enhance upland biodiversity, but grazing is not the sole driver. Landscape-scale studies are necessary to place into context detailed information on mammalian herbivore - vegetation - arthropod interactions.

The diversity of ground beetles, plant hoppers (Homoptera: Auchenorhyncha) and spiders (Araneae) in grassland, heathland and montane ecosystems is related to botanical diversity and the structural variability of vegetation [13, 49,50,46 30,58]. For grasslands in general, there is a positive correlation between the number of botanical species and the species richness of bees (Hymenoptera: Apidoidea), butterflies (Lepidoptera), phytophagous beetles (Coleoptera: Chrysomelidae) and true bugs (Hemiptera)[48]. Differences between insect and arachnid species in the effects of grazing are highlighted by work undertaken in Wytham Woods, Oxfordshire [51,42,47]. For spider assemblages, changes in plant architecture were found to be most important, while other species (e.g. leaf miners) were affected more by variations in floristic species composition. As a consequence, leaf miners had a rapid turnover whereas spider species accumulated over time. Age of grassland was also important; there are common species of spiders, leaf miners and leaf hoppers (Cicadellidae) that are restricted to old grasslands.

The structural complexity of tussock-forming grasses encourages more planthoppers and web-building spiders in upland grasslands [52]. For wolf spiders (Araneae: Lycosidae), species which pursue prey and do not build webs, the reverse is true and ca. 92% of individuals of this family mainly use the shorter grass between tussocks [54]. The relationships between grazers, vegetation and arthropods for upland, indigenous grasslands were consistent with the situation in lowland grasslands. The diversity of many arthropod taxa of lowland grasslands were favoured primarily by an increase in average vegetation height [53; 42;47, 55].

Although general arthropod diversity is diminished by intensive management, many species respond within a few years to favourable changes in vegetation structure and botanical species composition that result from modified management [56,51,42,57,30]. Similarly, Coleoptera (beetles) of lowland grasslands are affected by the intensity of pasture management and species of ground beetles (Carabidae) have been identified that are resilient to or excluded by such management [36,57,10]. The indicator species of intensively managed, lowland pastures are typically smaller [33] and more mobile [58] than those of less intensively managed pastures. However, the inheritance effects of drainage, fertilizer and lime inputs, and the cultivated pasture may constrain the benefits to arthropod diversity of altered management of intensified pastures compared with indigenous grasslands.

To conserve arthropod diversity in grasslands used for livestock production, whether lowland or upland, rotational grazing management is advocated [12,59,60,29,32]. This would provide habitat for those species requiring short swards and intense grazing, as well as large, diverse invertebrate assemblages in the taller, older swards. A mosaic including patches of grassland that have been ungrazed for two to 15 years may be optimum for conservation of grassland invertebrates [61,12]. This is comparable with the conservation management of Dutch salt marsh grasslands recommended by van Wieren [62], that grazing should be between the level at which all grass is grazed short, and the level at which parts of the grassland become rank. In such conditions the grassland naturally becomes a mosaic of areas of short and tall grass and it was recommended for the Dutch grasslands that management should achieve an optimum ratio of 1:1 between these components. Further research is required to assess whether such mosaics are appropriate to sustain populations of various arthropod species typical of upland grasslands and heaths.

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